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The Natural History of the Oilbird, *Steatornis caripensis*, in Trinidad, W. I. Part 2. Population, Breeding Ecology and Food[1,2,3]

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(Plates I-IV; Text-figures 1-4)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction of the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, Zoologica. 1952, 37 (13: 157-184.]

The Trinidad Population

THERE are at present eight known Oilbird colonies in Trinidad, in caves ranging from sea level to about 2,500 feet (Text-fig. 1, Table I). The four best known have been the subject of numerous accounts, ornithological and popular (*e.g.*, Kingsley, 1871 (Huevos); Chapman, 1894 (Huevos); Cherrie, 1907 (Aripo "Main Cave"); Roosevelt, 1917 (Oropouche); Williams, 1922 (Arima, Oropouche); Hollister, 1926 (Arima, Huevos); Myers, 1935 (Arima); Sanderson, 1940 (Aripo "Main Cave"). I have found no published account of La Vache cave and the smaller Aripo caves. In addition, at least five small colonies, four of them in sea caves, have been exterminated in recent years as the result of raids by fishermen and others. These also are listed in Table I. It is rather unlikely that any important colony remains undiscovered, but not impossible that in the limestone of the Aripo massif there may be small undiscovered colonies. Some of this country, which is honeycombed with small caves, is difficult to penetrate and not much visited.

I was able to visit all the known colonies, some of them several times, and made an attempt to assess the present adult population (Table I). Direct counting of all the adults is impossible in most of the caves; instead, it is necessary to count all the nests which appear to be occupied, count all the birds that can be seen perched on nests and ledges, estimate the number of birds flying about, and from these figures assess the number of birds present. I think it unlikely that the estimated total of 1,460 adults is out by more than 500 either way.

Such a small population of a very specialized bird is highly vulnerable, and indeed the extinction of five colonies is evidence that the Trinidad population has been reduced in recent times. None of these exterminated colonies can, however, have been very large. The larger Trinidad colonies, like those in Venezuela, have persisted for years in spite of constant exploitation by man. Though their numbers have probably been reduced, they are certainly under no immediate threat. As long as the forest remains, which provides the Oilbirds' food, the steady harvesting of a proportion of the young birds, though deplorable, is no danger to the survival of the

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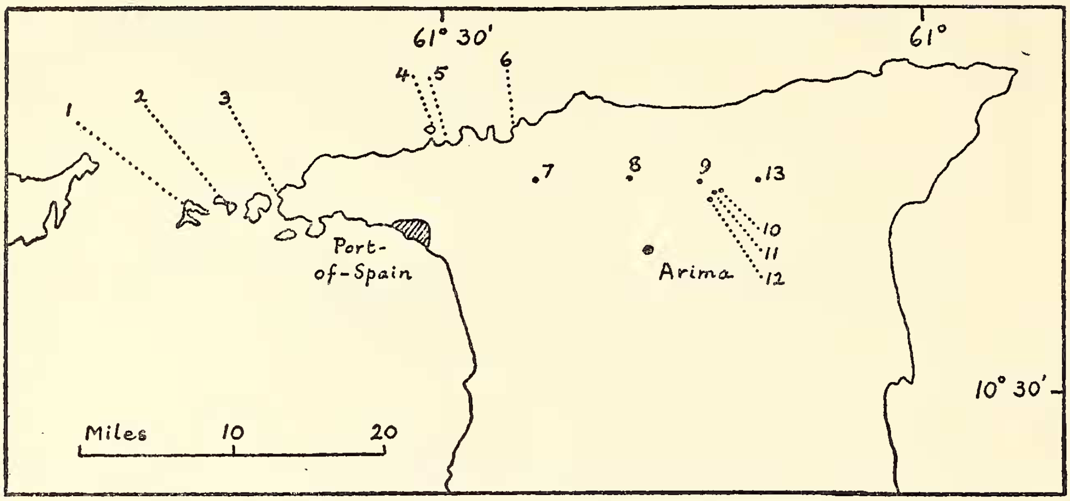


TEXT-FIG. 1. Trinidad Oilbird colonies. **1**: Chacachacare (extinct). **2**: Huevos. **3**: L'Ance Pawa (extinct). **4**: Saut d'Eau (extinct). **5**: La Vache. **6**: Maracas Bay (extinct). **7**: Acono (extinct). **8**: Arima gorge. **9**: Aripo main cave. **10**: Aripo well cave. **11**: Aripo middle cave. **12**: Aripo small cave. **13**: Oropouche. For further details see Table I.

species. A more real danger may come from the mounting pressure of the human population on the surviving areas of forest. It is to be hoped that future governments will both conserve the forests and protect the birds.[4]

The Arima gorge colony is known to have fluctuated greatly. During the present study there have usually been 25-30 adults present, and the number of breeding pairs in the years 1957-62 has been as follows: 11, 13, 9, 9, 8, 11. The breeding population cannot in fact rise much above the 1958 figure, as there are not more than 15 or 16 suitable nest-sites. In September, 1959, the colony was raided by a poacher; at least eight adults were killed and for some weeks the cave was almost deserted of birds. Gradually the survivors returned, until by December, when breeding began again, there were 14 birds, and a little later 21 birds were present. At various times in the past the numbers reported have been very low, probably as a temporary result of the same cause. Clearly this colony could easily be exterminated by steady persecution.

The Annual Cycle of Breeding and Moult

There has hitherto been no exact information on the Oilbird's breeding season, for either Venezuela or Trinidad. Most naturalists have visited the colonies in the first half of the year, especially from March to May when the birds are known to be nesting. There is a widespread belief in Trinidad that May is the month to collect young birds; luckily for the birds, this is only partly true. May is a good month, but other months may be equally good.

Table II shows that in the five years 1957-1961 clutches were started in the Arima colony in every month except October and November, with 87% of the total in the six months December-May. There is a distinct annual breeding season, with a very variable start. In three years the main period of laying started in December, in one year in January (1962, for which records were obtained up to the end of May), and in two years in March. In each year several nests started within a week or two of each other, and the later nests in the following few weeks. There seems no doubt that some kind of mutual stimulation is involved in this synchrony.

Limited information on other colonies has indicated breeding seasons similar to that at the Arima gorge colony. But there are not many caves where it is at all easy to inspect the nests, and information is very incomplete. Also, these other caves are regularly disturbed by poachers, so that the normal breeding season may be obscured. Thus visits to La Vache cave in 1958, the Huevos cave in 1959 and the Aripo Well cave in 1960 and 1961 all indicated a breeding season similar to that at the Arima gorge in the

[4]Oilbirds are protected by law in Trinidad, but the law is not enforced and would be difficult to enforce. The Aripo, La Vache and Huevos caves are still regularly raided. The Oropouche cave is on private land and the owners are trying to protect it, but it is not difficult for poachers to enter unobserved and they apparently still do so. The Arima gorge colony is also on private land and is protected by the owner.

same year; but on another visit to the Aripo Well cave in March, 1959, when breeding was just beginning in the Arima gorge (Table II), six of the ten nests whose contents could be seen contained young of a size that indicated egg-laying in December and January.

Intervals between Broods and Sequence of Broods.—The limited evidence suggests that undisturbed pairs retain their nests year after year. One banded bird was seen on the same nest in three successive years, and another in two successive years. Unfortunately the raid on the cave in September, 1959, when a number of adults were killed, probably including two banded ones, put an end to these observations, but they suggest that successive clutches in the same nest are normally laid by the same female, and this has been assumed unless there was evidence to the contrary.

On this assumption, an analysis has been made of the intervals between the ending of one nesting attempt and the laying of the first egg of the next clutch, excluding intervals spanning the time of the raid on the cave. Table III gives the 47 intervals that are available for analysis. It will be seen that nesting attempts that ended in failure in the months December-May were nearly all followed by a new clutch after intervals ranging from 19 to 75 days (mostly 19-33 days). Those that ended in failure in the months June-October were nearly all followed by intervals of several months, during which the pair concerned probably moulted (see next section), leading to re-laying in the following breeding season. The intervals following successful nesting attempts were less consistent. Those that ended in the months April-August were followed either by intervals of less than 34 days, leading to a further attempt in the same breeding season, or by long intervals of several months during which the pair probably moulted, leading to re-laying in the next breeding season. Among

Table I. Present Colonies of Oilbirds in Trinidad and Their Populations

Colony	Population
Oropouche cave	200
Aripo caves	
"Main cave"	400
"Small cave"	10
"Middle cave"	140
"Well cave"	80
Arima gorge (Spring Hill cave)	30
La Vache cave	300
Huevos cave	300
	1460

Notes on Colonies

Present colonies:

Oropouche cave. Extensive limestone cave formed by stream flowing out of hillside through narrow entrance. Nests from half-light near entrance to total darkness of furthest large chamber. Population based on count of birds leaving the cave in the evening (Part 1, p. 33).

Aripo main cave. Large limestone cave with wide entrance and stream flowing down into cave. Most nests in subdued light near entrance. Population estimate based on adults seen in cave and occupied nests.

Aripo small cave. Small limestone cave with dry floor; nests in subdued light. Counts on three visits: 12, 12 and 10 birds.

Aripo well cave. Dry limestone cave with top entrance. Some nests in almost full daylight, possibly even receiving a little sunlight. Population assessment based on counts of birds on nests and ledges.

Arima gorge. Partially covered-over gorge with stream flowing through. Adult population usually 25-30.

La Vache cave. Sea cave. Single large vaulted chamber about 75 feet high, with semicircular entrance 20 feet high. Assessment based on estimates of flying and perched birds on three visits.

Huevos cave. Sea cave. Single long chamber about 100 feet high, with entrance 15 feet high. Assessment based on direct count of 230 perched birds, with allowance for some flying and others perched out of sight.

Extinct colonies:

Chacachacare. Small sea cave on west side of island. Remains of nests and a few dry seeds found by Dr. T. H. G. Aitken, November, 1958. No further details known.

L'Ance Pawa. Sea cave about quarter of a mile to seaward of L'Ance Pawa Bay. Contained about a dozen or 20 birds in 1918 (Williams, 1922). Deserted in 1960, and no sign of recent occupation.

Saut d'Eau. Open sea cave on northeast side of Saut d'Eau Island, with a short tunnel through the cliffs. According to local information, occupied ten or twenty years ago but found deserted in 1960 and apparently had been for several years.

Maracas Bay. Small sea cave a short distance east of Maracas Bay. Deserted in 1957; some remains of old nests found. According to local information, had been occupied some 15 years previously.

Acono cave. Gorge in Acono Valley. Occupied in nineteenth century (Wall & Sawkins, 1860); deserted in 1918 (Williams, 1922).

TABLE II. BREEDING SEASONS OF OILBIRDS IN THE ARIMA GORGE COLONY
Numbers of clutches started in each month

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1957[1]	–	–	4	5	2	–	2	1	1	–	–	4
1958	2	1	8	1	4	2	–	–	–	–	–	–
1959	–	–	3	3	3	–	1	2	–	–	–	1
1960	3	4	–	1	1	–	–	–	–	–	–	3
1961	2	2	1	–	1	–	–	–	–	–	–	–
1962[2]	5	1	4	3	1							
Totals 1957-61	7	7	16	10	11	2	3	3	1	–	–	8

[1]Visits did not start until March 20, 1957. There were then no nests that could have started in January or February, but it is possible that some had started and already lost their contents by March 20.

[2]The 1962 records were obtained by Mr. J. Dunston, who inspected the cave regularly from the end of September, 1961, to June, 1962, after my own observations had ceased. These extra 14 nests are not included in the analyses of clutch-size, breeding success, etc., given elsewhere in this paper.

the short intervals there were two cases of the first egg of a new clutch being laid, in one case about 13 days before, and in the other case at about the same time as, the departure (from the same nest) of the last young of the previous brood. Those nesting attempts that ended successfully in the months October-January were followed mainly by intervals of intermediate length, leading to re-laying early in the following breeding season.

A complete nesting cycle, from the laying of the first egg to the fledging of the last young, lasts about five months (Part 1, p. 39). Thus with a short interval between broods it is just possible to rear two broods in a year, and this was in fact achieved by three pairs during the present study. One of these reared two broods between early December and the following October, having also reared a brood between April and September of the previous year. Thus they reared three broods in eighteen months. After the last they had an interval of 13 months before the next clutch was laid. Another pair, having completed the rearing of two broods between December and October, laid a new clutch in December, after an interval of 49 days, certainly not long enough for the moult. This brood was also successful and fledged in the following May, so that three broods were again reared in 18 months. There was then an interval of eight months before the next clutch was laid in the following January. The third pair reared two broods between March and the following January; they then had a gap of five months before the next clutch was laid, in late May but this failed and the sequence was broken. The data are insufficient for a proper analysis, but they suggest that pairs breeding successfully can rear two broods in a year only every second or third year. Discussion cannot be taken any further without considering the relation between breeding and the moult.

The Moult.—At every visit to the colony, all moulted flight-and tail-feathers were collected. Most of the moulted feathers are dropped outside the cave, presumably during feeding, but enough are dropped inside the cave to give an indication of the amount of moulting taking place in the colony. Nearly all were found on the slopes below the nests and could not be allocated to known nests.

Moulting takes place in every month of the year, but there is a well-marked seasonal variation. There is most moulting in the six months June-November (72% of all moulted feathers being found in these months) and least moulting in the six months December-May. Thus there is an inverse correlation between egg-laying and moulting, but nevertheless enough moulting takes place in the months December-May to make it very likely that some birds at least undergo moult while breeding. Examination of specimens suggests the same. Thirty-five dated Trinidad specimens have been available for examination (13 in the American Museum of Natural History, 11 in the British Museum and 11 trapped or collected during this study). Twenty-six were collected in the months January-May, the main egg-laying period, and 16 of them were undergoing moult of the primaries. The remaining nine were collected in July-October, and seven of them were moulting their primaries.

The sequence of moult is variable and sometimes irregular. Of 29 Trinidad specimens which were in wing-moult (those mentioned above and some undated specimens), 14 appeared to be undergoing a normal replacement of the primaries from the inner end of the row out-

TABLE III. INTERVALS BETWEEN BROODS
(Length of time between ending of one nesting attempt and laying of first egg of next clutch)

Month in which nesting attempt ended	Intervals of less than three months (in days)	Intervals of more than three months (in months)
January	—	5
February	*23*, **25**	—
March	*24*	—
April	—	8½
May	0, **19**, **19**, **20**, *23*, 33, **47**, **65**, *75*	9
June	*44*	6, 6, 6½, 7, 7, 7, **9**
July	—	6½, **7**, 8, **8½**, 9½
August	–3, 25	5, 5, *6½*, 7, *7½*, 8
September	76, 78, 84	3
October	49	4, *5½*, 7, 15
December	*24*, *72*	—

NOTE: Figures in ordinary type: previous nesting attempt successful. Figures in *italic* type: previous nesting attempt ending in loss of eggs. Figures in **heavy** type: previous nesting attempt ending in loss of young.

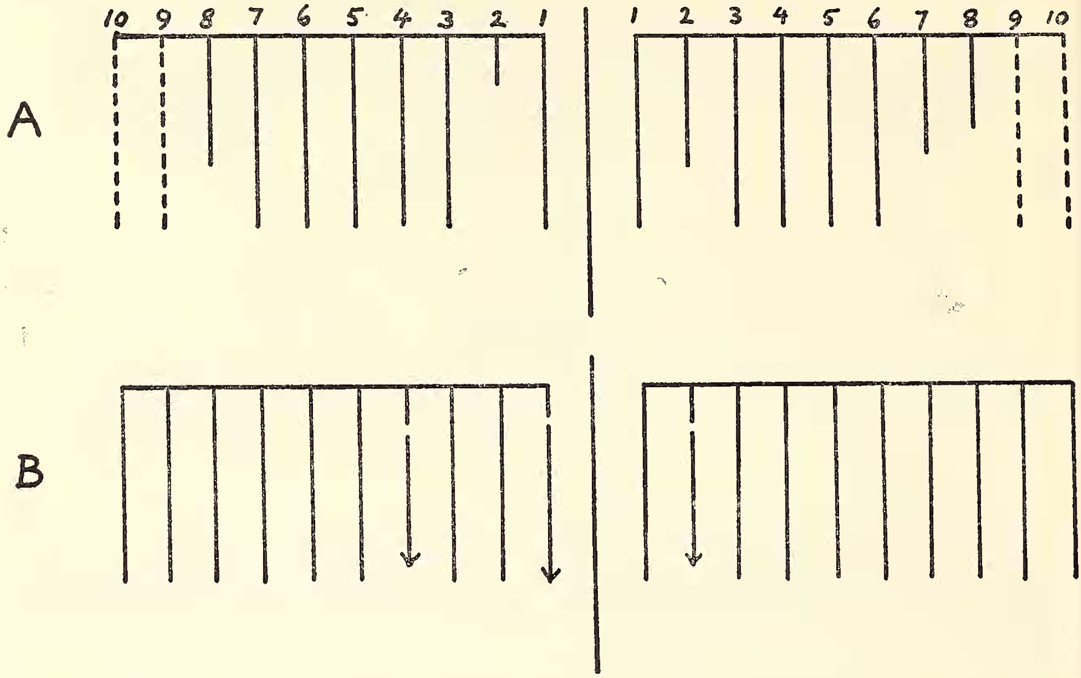
wards. Four other birds showed a similar condition, except that the moult of one wing was one or two feathers in advance of the other. The remaining 11 birds showed more complex or irregular conditions. In six, one wing was moulting but not the other, and in one of these moult was occurring in two separate places in the row. The remaining five all showed moult in two separate places in the row in at least one wing, and in one bird three feathers in the same wing (primaries 1, 6 and 9) were all in various stages of growth.

The most reasonable explanation for the presence of growing feathers at two separate places in the row seems to be that a second moult of the primaries had started before the previous one was complete. The clearest case was that shown in Text-fig. 2a, where a second moult had apparently started when the previous one was about half completed. Another bird was similar, except that the two wings were at slightly different stages. A third case, shown in Text-fig. 2b, was the bird mentioned later in this section, which was caught twice while moulting, and another showed an exactly similar condition, including the asymmetry between the two wings, except that the moult was at a slightly later stage. Alternatively, it may be that the moult sometimes starts simultaneously at two "foci" and proceeds outwards from these two points. Parallels for both conditions can be found in other birds; *e.g.*, overlapping successive moults in boobies (Dorward, 1962), multiple "foci" in birds of prey (V. & E. Stresemann, 1960).

The length of time needed for a complete moult must be several months. Examination of specimens showed that altogether there were only seven instances of two adjacent primary feathers growing, as against 51 instances of a single feather growing, in many cases nearly full-grown. Thus (unless moult starts at two foci) replacement of the whole series of ten primaries must on average take nearly ten times the length of time needed for the growth of a single feather. One individual of the Arima gorge colony was caught twice during the same moult, at an interval of exactly four weeks. Of the three feathers which were one-quarter grown on April 21, one was full-grown and the other two nearly full-grown on May 19 (Text-fig. 2b). If this bird was typical, more than ten months would be needed for a complete moult of the primaries, and even with moult starting from two foci not less than six months would be required.

Table III shows that several of the long intervals between nesting attempts were of less than six months, so that for these birds the moult must surely have overlapped the previous or subsequent nesting cycle, and since six months is probably an underestimate for the period of the moult, others may have done so as well.

The possibility must be considered that the rate of moult is variable; in particular, that it is faster during the off-season and slows down



TEXT-FIG. 2. Stages of primary moult in two Oilbirds. The ten primaries are shown diagrammatically from above, as follows: solid lines, complete or growing feathers, not recognizably old; broken lines, recognizably old feathers; arrows, amount grown between first and second captures (see text).

when the bird is breeding. Even without any connection between the timing of the onset of the moult and the breeding cycle, such a variation in rate of moult could account for the fact that moulted feathers were found in all months, but nearly three times as numerously in the months July-November as in the months December-May.

To summarize, the data show that the moult mainly occurs in the six months June-November, coinciding with the long intervals following nesting attempts that end in those months, and the evidence suggests that the moult of each individual lasts for several months and may overlap the nesting cycles. The possibility of variation in rate of moult according to the state of breeding must also be borne in mind. More definite conclusions are not warranted on the present evidence. Far more captures of birds with known nesting histories would be necessary to establish the exact relationship between breeding and the moult. Since it was found that the capture of adults had a disturbing effect on the whole colony, it was not practicable to obtain more than these fragmentary data.

Clutch-size

Clutches numbered from one to four eggs. Of the four one-egg clutches, three were laid by the same bird, perhaps a young bird breeding for the first time (see next section). The mean size of the 59 completed clutches was 2.7 eggs (Table IV).

Mean clutch-size decreased in the course of the breeding season from just over three to two eggs, 10 of the 11 clutches of four eggs being laid in the early part of the breeding season (December-March). It will be shown later that most food is available in the months March-June (Text-fig. 4), the period when most of the young from the early clutches are in the nest. It is reasonable to suppose that the seasonal variation in clutch-size may be adapted to the seasonal change in the food supply, as has been found for many north-temperate birds (*e.g.*, Lack, 1954).

Breeding Success

In the five years of observation, nearly half of the nesting attempts produced flying young. There were 68 nesting attempts (in which at least one egg was laid); 45 of these reached the hatching stage (and four more may have done so, the eggs or young disappearing around the hatching time); and of these, 31 reached the fledging stage, producing a total of 60 young. The earlier nests were more successful than the later ones, 21 out of the 38 nests starting in the months December-March producing fledged

Table IV. Clutch-size

	Number of eggs in clutch				Mean clutch-size
	1	2	3	4	
December		1	2	3	3.1
January	1	2	1	3	
February		1	4	2	2.7
March	1	7	6	2	
April		4	5		2.4
May	1	5	2	1	
June		2			(2.0)
July	1	1			
August			1		
Total (59)	4	23	21	11	2.7

young, compared with 10 out of the 30 starting in April-September. These figures are too small to be convincing of themselves, but the difference is probably real and due to the nesting behavior becoming less efficient as the season advances. Thus there were seven instances of eggs being deserted or lost soon after laying in the months April-September, and only two in the months December-March. There was an unbroken run of successes at only one nest, probably kept by the same pair throughout the period. At this nest there were five successful nestings, producing nine flying young. (This was one of the nests mentioned earlier, in which three broods were reared in 18 months). No nest had an unbroken run of failures, though some nearly did. In some cases a sequence of failures probably represented the first nesting attempts of a young pair. Thus at one nest four failures were followed by two successes, the clutch-sizes for this sequence being 1, 1, 1, 2, 4, 3.

Table V shows the fate of the 171 eggs laid. For nine clutches there was uncertainty as to the number of eggs laid, due to the disappearance of the clutch during laying. In these cases the greatest number known to have been laid has been counted. For others there is uncertainty as to the number of young hatched, owing to the disappearance of an egg (or young) at about the time that hatching was due. As unhatched eggs were known in several cases to remain in the nest long after the others had hatched, and several young were known to have died soon after hatching, it is likely that in most of these uncertain cases the eggs did in fact hatch.

The causes of egg failure were various. Sometimes an adult may kick off an egg as it flies from the nest. This was seen to occur once and it probably accounted for several other egg losses. Three times nests were flooded by water seeping through cracks in the rock during very wet weather and the eggs were chilled and eventually thrown out by the owners. Many other egg losses were unaccounted for; a few of these may have been caused by the crabs (*Pseudothelphusia garmani*) which occasionally walked over the nests and probably attacked the young.

Nearly 60% of the young known to have hatched reached the flying stage. As with eggs, the causes of failure were mostly unknown. Most died in the early stages, and it is probable

Table V. Hatching and Fledging Success

Eggs/young present		Losses	
Eggs laid	171	Deserted without being incubated	2
		Flooded; thrown or washed out	7
		Kicked off by adult	1
		Used for egg-white sample	1
		Disappeared before possible hatching date (cause unknown)	31
Eggs remaining at hatching time	129	Infertile	7
		Deserted	1
		Flooded and chilled; embryo killed	1
		Died during hatching	1
		Disappeared at hatching time; not known if hatched or not	16
Eggs hatched	103	Lost at ages 0-20 days	21
		Lost at ages 21-40 days	15
		Lost at ages 41-60 days	2
		Lost at ages 61-80 days	4
		Lost at 80+ days	1
Young flying	60		

that competition for food with their older nestmates was an occasional cause of death at this period (Part 1, p. 41); there was no evidence of starvation in the later stages. Three young were almost certainly killed by crabs, the corpses of two of them being found on ledges near by, partly eaten. (Large crabs had been seen frequenting this and other nests, and no other potential predators could be found. When the holes in which the crabs lurked were blocked up, no other deaths of this kind occurred). Four young fell from their nests when part of the structure collapsed. In addition one fell from an intact nest and it is almost certain that others did. There was no evidence of predation of the young by man during the period of the study.

Food: General Remarks

There have been no detailed studies of the Oilbird's food. Most authors have stated that they feed mainly on the fruits of palm trees, while some have remarked that the family Lauraceae is also important. McAtee (1922) lists some seeds found in a Trinidad colony and refers to earlier accounts, pointing out that these may be of doubtful value owning to uncertainty of identification. For Venezuela, Pietri (1957) lists several species of palms, two species of Lauraceae and one of Burseraceae, and says that probably other kinds of fruit are eaten.

The feeding habits have been described in Part 1, pp. 31-32. Here it may be recalled that the birds pluck fruit in flight, at night, swallowing them whole. Nearly all the fruits taken have a firm pericarp enclosing a single rather large seed. Only the pericarp is digested, the seeds being later regurgitated intact.

In the course of the present study, regurgitated seeds were collected regularly at the Arima gorge colony from April, 1957, to September, 1961, samples of several hundreds, sometimes several thousands, being taken in each month. Most were collected from catching trays slung on the slopes below the nests, and others from the nests themselves. Care was taken to collect only freshly regurgitated seeds. Altogether, over 112,000 seeds were collected and examined. Samples were also collected from other caves as opportunity arose.

The identification of seeds in an area of rich tropical forest presents some difficulty. A few kinds, especially the distinctive seeds of some common palm species, were soon identified. Others remained unidentified for a long time, but in nearly every case the tree was eventually found in the forest. Two species were identified from herbarium material on the basis of whole fruits and seeds collected in the cave. In the end only one important food tree remained unidentified. For the study of Oilbirds' food it is unfortunate that the Lauraceae is taxonomically a difficult family. There are many species with rather slight differences between them, and even in the important national collections there is a shortage of good material with mature fruits.

An incidental outcome of this study was the discovery of some species of Lauraceae new to Trinidad. *Beilschmiedia sulcata* represents a genus and species new to the island; *Licaria guianensis* and *Ocotea caracasana* were previously unrecorded from Trinidad; and specimens of an undescribed species, since named *Ocotea trinidadensis* Kostermans, were collected in the course of examining Lauraceae in the forest, though its fruit was not recorded in the Oilbird's food.

Composition of the Food

Table VI gives the totals of all the seeds collected from the Arima gorge colony throughout the period of the study. Eighteen species were important (over 100 seeds collected): 7 palms, 8 species of Lauraceae, 2 species of Burseraceae, and one species of Araliaceae[5]. Numerically, the Burseraceae outnumbered the Lauraceae in spite of the small number of species. Text-fig. 3 gives outline drawings of the more important seeds, with descriptive notes, and six kinds are illustrated in Plates I-III.

Most of the fruits eaten were regularly seasonal. This was especially true of the Lauraceae, which with only one exception showed clearly defined fruiting seasons varying little from year to year.

Palms.—The two important palms *Euterpe langloisii* and *Jessenia oligocarpa* were the two striking exceptions to the general rule that the food trees are seasonal in their fruiting. Seeds of *Euterpe* were present in every sample, and in many samples they outnumbered all other seeds (Table VIIa). *Jessenia,* a much larger fruit, was always present in much smaller numbers, and there was one long period, from November, 1959, to July, 1960, when it was very scarce and failed entirely for three months (Table VIIb). During this period, no trees in the forest could be found with ripe fruit.

In these two palms, each tree bears inflorescences and bunches of fruit in various stages of growth, and field observations showed that the fruit ripens very slowly. In addition, the ripe fruit has a hard and dry pericarp and probably

[5]Wrongly described in Part 1, p. 42, as probably myrtaceous.

remains in an edible condition on the tree for many weeks. Thus these two palms normally produce a rather constant supply of ripe fruit throughout the year. The cause of the general failure of *Jessenia* in 1959-1960 was not discovered; probably unsuitable weather some time previously had led to a gap in its flowering.

Euterpe is abundant in the forests of the Arima Valley, but *Jessenia* is rare, having its center of abundance in more low-lying swampy forests five or ten miles to the southeast. This is probably the main reason why the seeds of *Jessenia* were always less numerous than those of *Euterpe.*

Bactris cuesa, a small forest palm of the under-story, is much more seasonal in its fruiting than *Euterpe* and *Jessenia* (Table VIIc). Its season was even more sharply defined than is suggested by the table, as most of the fruits collected in the samples before May were unripe and regurgitated intact.

Roystonea, which was collected regularly in small numbers in the samples, does not grow in the Arima Valley. Its natural habitat in Trinidad is the low-lying swampy forest near the east coast, especially the Nariva Swamp, but it has been much planted in gardens and parks and the Arima gorge birds probably obtained its fruit from the town of Arima, five miles away. Table VIId shows that it was found in the samples in all months of the year.

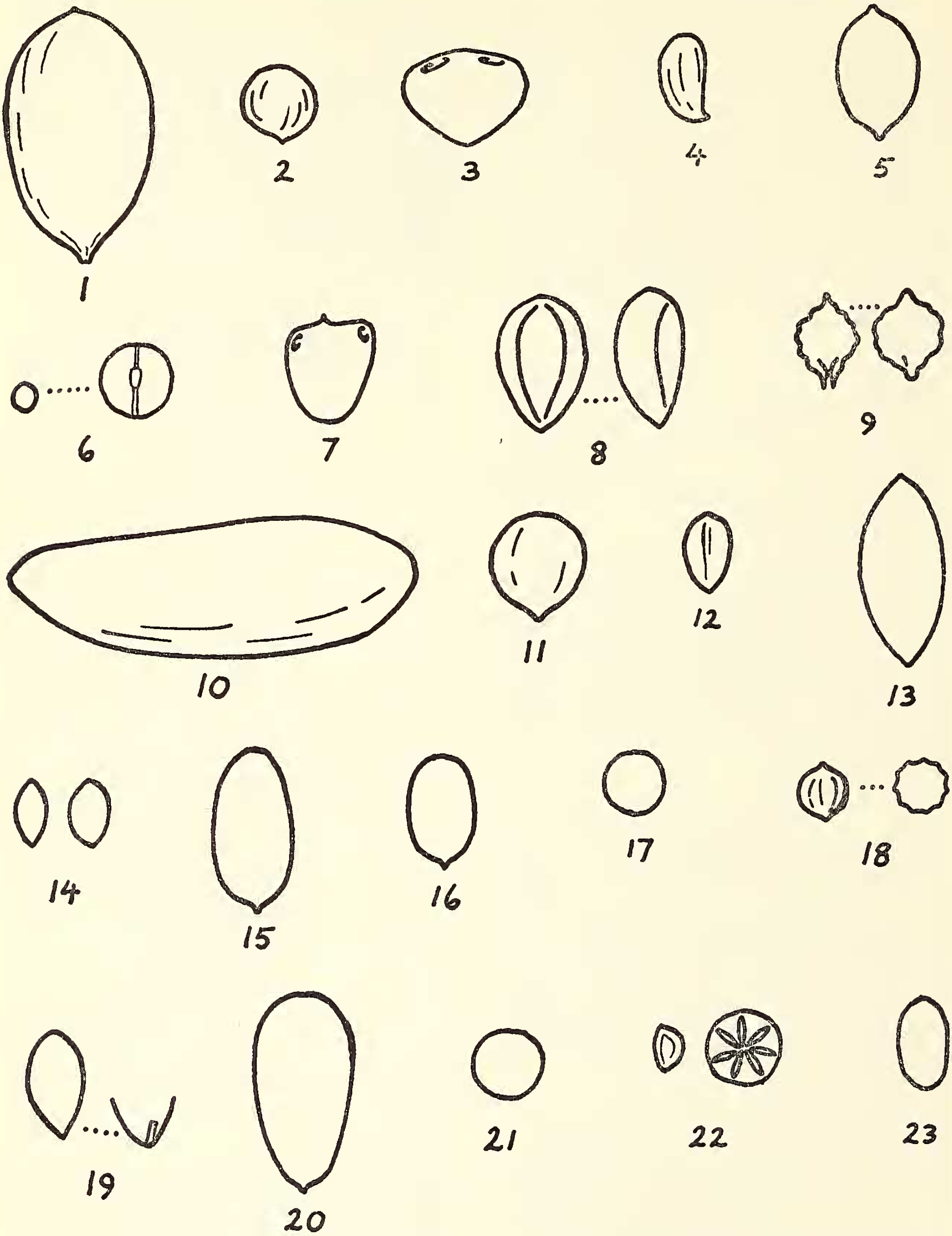
Livistona chinensis is an introduced palm. It probably does not grow nearer to the cave than Arima, where it has been planted in small numbers. October to April are the main months for ripe fruit. Seeds of *Livistona* were found in moderate numbers in the samples from 1957 to April, 1959, but not thereafter. Probably this reflects a temporary habit of a few birds, or possibly the individuals visiting the *Livistona* trees were among those killed in the raid on the cave in September, 1959; the trees fruited abundantly in Arima in the two subsequent years.

Geonoma vaga is a small palm of the forest undergrowth, growing to about 12 feet. Its fruits are very small (about 4 mm. in diameter), the hard seed being covered by a thin pericarp. Like *Livistona,* it too was found in the samples only up to 1959, in the months January-July. It is remarkable that Oilbirds should be able to take its fruit at all, as it grows chiefly along streams and gullies, in rather dark parts of the forests, and surprising that they should have found it worth while to do so. Possibly one or two trees growing near the cave mouth were occasionally visited by the birds as they entered or left the gorge.

Unripe fruits of species of *Bactris* type were found in the samples somewhat irregularly but in all months of the year, occasionally amounting to an important fraction of the total food. The fruits were small and soft, without a seed, and many were regurgitated whole or only slightly broken up. Identification of most of them was uncertain, but probably the great majority were immature fruits of *Bactris gasipaes* (locally known as Pewa), a palm that is cultivated in small numbers for its edible fruits. In addition to the mature fruits, which contain a

TABLE VI. TOTAL NUMBERS OF FRUITS REPRESENTED IN COLLECTIONS FROM THE ARIMA GORGE COLONY, 1957-1961

PALMAE	*Euterpe langloisii*	45,520
	Bactris cuesa	6,315
	Jessenia oligocarpa	4,669
	Unripe *Bactris* sp.	663
	Livistona chinensis	489
	Roystonea oleracea	327
	Geonoma vaga	165
	Bactris sp.	17
	Desmoncus sp.	6
	Aiphanes sp.	3
	Bactris sp.	2
	Total	58,176
LAURACEAE	*Ocotea wachenheimii*	9,880
	Cinnamomum elongatum	5,831
	Ocotea caracasana	3,853
	Nectandra martinicensis	2,846
	Ocotea oblonga	2,370
	Nectandra kaburiensis	290
	Aniba firmula	267
	Nectandra membranacea	149
	Aniba trinitatis	70
	Aiouea schomburgkii	68
	Licaria guianensis	12
	Nectandra sp.	4
	Beilschmiedia sulcata	3
	sp. indet.	2
	Ocotea canaliculata	1
	Total	25,646
BURSERACEAE	*Dacryodes* sp.	21,895
	Trattinickia rhoifolia	6,731
	Protium sp.	1
	Total	28,627
ARALIACEAE	sp. indet.	148
OLEACEAE	*Linociera caribaea*	50
MYRISTICACEAE	*Virola surinamensis*	10
ANACARDIACEAE	*Tapirira guianensis*	7
SAPOTACEAE	*Pouteria minutiflora*	3
BORAGINACEAE	*Cordia bicolor*	1
MALPIGHIACEAE	*Byrsonima spicata*	1
UNIDENTIFIED	Several species	48
	Total	268
	Grand Total	112,717



TEXT-FIG. 3. Seeds of the chief fruits eaten by Trinidad Oilbirds. (All natural size except where indicated.)

1. *Jessenia oligocarpa* (palm). Hard and fibrous, streaked dark and pale brown (see also Plate I).

2. *Euterpe langloisii* (palm). Hard and fibrous, pale yellow-brown. When dry, fibers curl off giving a hairy appearance (see also Plate I).

3. *Bactris cuesa* (palm). Hard and blackish, sometimes with pale fibers adhering; three pits (germ-pores) on the flattened end.

4. *Roystonea oleracea* (palm). Distinctively boat-shaped; pale fibrous surface, the fibers not coming away.

5. *Livistona chinensis* (palm). Smooth, hard, whitish, non-fibrous surface, with slight points at both ends, and slightly ridged down opposite sides (see also Plate II).

6. *Geonoma vaga* (palm). Hard and smooth; dark brown, with a pale apical spot and a pale longitudinal streak all the way round. (Left, natural size; right, enlarged.)

7. Unidentified *Bactris* sp. (palm). Hard and blackish, with three germ-pores, two with ridges above.

8. *Dacryodes* sp. (Burseraceae). Whitish, soon becoming stained, with demarcated "panel" becoming detached when the seed dries. When fruit is mature, seed contains seedling coiled up within.

9. *Trattinickia rhoifolia* (Burseraceae). Hard, brown; with two points at one end and one at the other, and complex ridges and depressions (see also Plate II).

10. *Beilschmiedia sulcata* (Lauraceae). Smoothish, pale brown; rather variable in shape and size, but typically very slightly curved. Soon splits into two halves (and germinates readily).

11. *Ocotea wachenheimii* (Lauraceae). Smooth, very slightly ridged; pale brown when fresh (see also Plate III).

12. *Ocotea oblonga* (Lauraceae). Dark brown, pitted with pale longitudinal streaks; fairly prominently ridged down opposite sides.

13. *Ocotea caracasana* (Lauraceae). Smooth, brown; regularly spindle-shaped.

14. *Cinnamomum elongatum* (Lauraceae). Smooth, pale to dark brown depending on maturity; somewhat variable in shape (two extremes shown); rather soft.

15. *Aniba firmula* (Lauraceae). Smooth, brown with blackish streaks; variable in size and shape, but with point at one end and rounded at the other, and usually broadest at pointed end (see also Plate III).

16. *Aniba trinitatis* (Lauraceae). Smooth, pale brown, unstreaked or faintly streaked; variable in shape, but characteristically widest near pointed end and often with slight ridges on opposite sides.

17. *Nectandra kaburiensis* (Lauraceae). Smooth, pale brown when fresh, nearly spherical; thin-skinned, with pinkish-purple endocarp.

18. *Nectandra membranacea* (Lauraceae). Brown, with slight points at both ends, and regular "fluting," as shown in transverse section.

19. *Nectandra martinicensis* (Lauraceae). Smoky brown, with black showing through in irregular longitudinal streaks. Slightly asymmetrical, one side more curved than the other, and apex with lip-like hilum (right, enlarged).

20. *Licaria guianensis* (Lauraceae). Smooth, dark brown, with point at narrow end; slightly ridged longitudinally; variable in size.

21. *Aiouea schomburgkii* (Lauraceae). Smooth, brown, mottled with dark markings; almost spherical.

22. *Araliaceae* sp. Seeds flattish, roughly half-moon shaped; embedded radially in berry as shown.

23. *Linociera caribaea* (Oleaceae). Pale brown, with a network of raised veining; bluntly oval.

large seed and are probably too large for Oilbirds to swallow, they produce small fruits that do not develop to maturity. One owner of a small estate told me that he had shot an Oilbird that was visiting his Pewa trees.

Besides these seven main kinds, there was a very small number of palm seeds of other species. Several seeds were close to *Bactris cuesa* but differed consistently in shape and probably represented other species. The taxonomy of this section of the genus is difficult, and there has been some fine splitting of species (Bailey, 1947). *Aiphanes* sp., ? *minima*, of which three seeds were found, is a cultivated species with edible fruits (locally known as "edible gri-gri"). Six seeds were referred to *Desmoncus*, a genus of spiny climbing palms, but they were not the common species *D. major*.

Lauraceae.—Table VIII shows the percentage occurrence of the ten most important species of Lauraceae in the food. With one exception (*Ocotea wachenheimii*), they all had well-defined fruiting seasons which were much the same in all years; in all but two of them the season fell mainly in the months March-June. One of the exceptions, *Aniba firmula*, fruited rather earlier, in December-April, while the other, *Nectandra martinicensis*, was the only species with a fruiting season at the end of the year, from September to November. Table X summarizes the fruiting seasons of these ten regularly occurring species, and shows clearly the importance of the March-June peak.

In number of seeds found in the samples, *Ocotea wachenheimii* was the most important species, and, as mentioned above, it was the only species with an irregular fruit season. In all years a main fruit season began in November

TABLE VII. SEASONAL OCCURRENCE OF PALMS IN THE FOOD SAMPLES

		Percentage of the total in the different months											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
(a)	1957	...	...	...	20	28	51	64	74	58	43	75	64
Euterpe	1958	26	33	31	28	31	18	16	37	46	53	45	4
langloisii	1959	9	44	54	49	26	28	6	2	36	32	41	82
	1960	40	15	37	58	52	21	15	16	30	54	78	86
	1961	62	54	73	56	45	44	30	6	21	...	...	...
(b)	1957	...	...	...	17	7	3	7	8	12	13	15	10
Jessenia	1958	5	6	2	1	1	2	4	11	12	7	8	2
oligocarpa	1959	6	14	25	20	5	3	3	1	2	1	+	+
	1960				+	+	+	+	1	9	12	11	9
	1961	3	1	1	1	2	6	5	2	3	...	...	...
(c)	1957	...	...	...		1	4	9	10	11	3	1	+
Bactris	1958	+	+	+	+	1	3	17	33	18	15	25	2
cuesa	1959			1	+	4	17	55	74	17	10		+
	1960	+		+	+	2	5	4	7	11	1		
	1961			+	+	+	5	23	29	16	...	...	...
(d)	1957	...	...	...		+	+	+	1	1	1	2	+
Roystonea	1958	+	+	+	+	1	1	+	+	+	+		
oleracea	1959			+		+				+		+	+
	1960		+	+	1	2	+				+		
	1961		+	+					+		...	...	...

Note (applying also to Tables VIII and IX): +, less than one percent. Dots (....), no sample collected. Where the year is omitted, no seeds were found in that year.

or December, which lasted from four to six months. In 1958 and 1960, and less markedly in 1961, there was a secondary minor fruit season in June or July. The fruiting period April-July, 1957, might have been either the tail-end of a long and prolific fruiting beginning at the end of the previous year, or it might have been a combination of such a fruiting with a secondary fruiting in June-July.

A single tree of *O. wachenheimii*, growing near the cave, was kept under observation from January, 1958, to September, 1961. It had ripe fruit regularly from late November or December to February, and had none in June or July. Another tree on an exposed ridge at a higher altitude, which was visited less regularly, had nearly ripe fruit in June in two years. Three out of the four samples of seeds taken from caves at the extreme western end of Trinidad in July and August had good numbers of seeds of *O. wachenheimii*, including one collected in 1959 when none were being taken by the birds in the Arima gorge. It seems probable that individual trees of this species have one main fruiting season per year, which may be either November-February or June-July, and it may be that the June-July fruiting season is more general in the drier parts of the island.

Beilschmiedia sulcata is not included in the ten main species of Lauraceae, as only three seeds were found in the Arima gorge (in March, May and June), but it is one of the most important fruits taken by the Oilbirds in the caves to the east of the Arima Valley. Fresh seeds were found in nearly every month of the year in these caves, but their presence was irregular. Thus there were good numbers in May and December, 1957, but none in December, 1959, or May, 1960. *Beilschmiedia* grows at high altitudes on the Aripo massif, where the rainfall is extremely high and probably less seasonal in its distribution than at lower altitudes, and the fruiting of trees may be less regularly seasonal.

Burseraceae.—The most important species, *Dacryodes* sp., fruited in alternate years during the period under study (1958, 1960 and 1962), very small numbers of seeds being found in the intervening years. It is a common tree above 1,500 feet in the Northern Range and when it was in fruit its seeds often outnumbered everything else in the samples. Individual trees remain in fruit for many weeks, as the fruits, borne in large bunches, ripen slowly and irregularly. In the intervening years, some trees that were examined produced fruit which grew to full size and looked normal but were in fact hollow. There was no evidence that these were taken by Oilbirds.

Table VIII. Seasonal Occurrence of Lauraceae in the Food Samples

		Percentage of the total in the different months											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ocotea caracasana	1957	.....	.....	.....	28	28	20	11	2	+	+		
	1958		+	3	1	1							
	1959		+	1	3	2	+						
	1960		+	2	1	+							
	1961		1	4	4	4	2				.....	.....	.....
Ocotea oblonga	1958			3	13	1		+					
	1959				21	17	1						
	1960				3	2							
	1961				3	7	4				.....	.....	.....
Ocotea wachenheimii	1957	.....	.....	.....	7	7	3	1	+				23
	1958	65	39	1				7	11	1		12	90
	1959	56	1										1
	1960	42	28	3	+		1	1	+			1	2
	1961	34	44	21	4	+		+			.....	.....	.....
Cinnamomum elongatum	1957	.....	.....	.....	16	18	10	+					
	1958					3	14	5					
	1959				3	41	15						
	1960			+	+	1	1						
	1961		+		27	37	9				.....	.....	.....
Nectandra martinicensis	1957	.....	.....	.....					1	11	28	1	
	1958									20	19	3	
	1959									26	50	56	2
	1960	+	+							11	22	5	
	1961								+	+	.....	.....	.....
Nectandra membranacea	1959				+	1							
	1961				3	1					.....	.....	.....
Nectandra kaburiensis	1957	.....	.....	.....		1	1	+					
	1958						1	+					
	1959					+	1						
	1960					+							
	1961					2	1				.....	.....	.....
Aniba firmula	1958	2	+										
	1959												+
	1960	+	3	4	+								
Aniba trinitatis	1958			+	+								
	1960		+	1	+								
	1961			+	1	+					.....	.....	.....
Aiouea schomburgkii	1958			1	1	1	2						
	1961				+						.....	.....	.....

Note: The following species never accounted for as much as 1% of the monthly sample: *Licaria guianensis* (found in May, 1958, and March-May, 1961); *Beilschmiedia sulcata* (found in March, May and June in three different years).

Trattinickia seeds were found in the food samples in nearly every month, but comprised an important fraction of the total only in the months June-September. A single tree kept under observation for over 2½ years fruited in 1959 and 1961, but not in 1960. After the first lot of fruit was gone most of the leaves fell and new flowers appeared seven months after the growth of the new leaves; the fruits then took ten months to ripen. The complete cycle took two years. Three other trees that were less regularly observed fruited at the same time as this

TABLE IX. SEASONAL OCCURRENCE OF BURSERACEAE AND ARALIACEAE IN THE FOOD SAMPLES

		Percentage of the total monthly sample											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Dacryodes	1957	....					+	+					
sp.	1958	+	18	57	56	62	60	47	5	+	1		
	1959				+								3
	1960	12	53	54	37	39	71	68	35	+			
	1961								+		....		
Trattinickia	1957	....			4	7	6	6	4	5	6	3	1
rhoifolia	1958	1	2	1	1	1	1	2	1	1	4	4	1
	1959	5	3	1	2	6	34	36	23	17	6	1	6
	1960	4	1	+	+	+	+	11	41	37	4	1	+
	1961	+	+	+		1	28	42	59	47	....		
Araliaceae	1957	....							+	1	+	+	
sp.	1958								+	+	+	1	+
	1959								+	2	1		
	1960							+	+	2	+		
	1961								2	7	....		

tree. But the continuous presence of *Trattinickia* seeds in the samples shows that other trees must have fruited in the intervening years. Like *Dacryodes, Trattinickia* trees remain in fruit for several weeks.

Araliaceae.—The only regularly eaten fruit that did not conform to the usual type (firm pericarp surrounding a single seed) remained unidentified. The tree was never found, and since the seeds were not found in any cave except the Arima gorge, though five samples were collected at other colonies at times when the seeds were regular in the Arima gorge samples, it is hard to avoid the conclusion that either the tree is very local or its exploitation is an idiosyncrasy of the Arima gorge birds. Occasional regurgitation of whole fruits enabled the family to be determined with reasonable certainty (see also Appendix).

Other Species.—*Byrsonima spicata, Virola surinamensis, Pouteria minutiflora, Tapirira guianensis* and *Cordia bicolor* are all common trees in the Arima Valley, and their fruits are much eaten by other kinds of birds. Their great rarity in the food samples indicates that Oilbirds in general avoid them. *Byrsonima, Cordia* and *Pouteria* all have more or less succulent, acid fruits, while *Virola,* the wild nutmeg, has a net-like aril enclosing the seed. All these are very unlike the sort of fruit usually eaten by Oilbirds. *Tapirira,* also a common tree, has a fruit that is superficially like that of *Dacryodes* and is much eaten by pigeons. The reason for its avoidance by Oilbirds is discussed in a later section (p. 217).

Only one tree of *Linociera caribaea* (Oleaceae) was found in the Arima Valley, and two others in a valley a few miles to the east. Thus

TABLE X. FRUITING SEASONS OF THE TEN MOST IMPORTANT SPECIES OF LAURACEAE

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Aiouea schomburgkii			×	×	×	×						
Aniba firmula	×	×	×									
Aniba trinitatis			×	×								
Cinnamomum elongatum				×	×	×	×					
Nectandra martinicensis									×	×	×	
Nectandra membranacea				×	×							
Nectandra kaburiensis					×	×						
Ocotea caracasana			×	×	×	×						
Ocotea oblonga				×	×	×						
Ocotea wachenheimii	×	×	×	×	×	×	×	×			×	×
Number in fruit in each month	2	2	5	7	7	6	2	1	1	1	2	1

it is not a common tree, and the presence of its seeds, in moderate numbers, in the food samples in one year only may indicate that a few birds found a tree but did not revisit it in subsequent years.

There was evidence of only one kind of fruit being eaten besides those found in the food samples. A reliable observer reported an Oilbird feeding on unripe fruits of the Tonka Bean (*Dipteryx odorata*) in an Arima garden. The mature fruit, about three or four inches long, is far too large to be taken. It is perhaps significant that the Tonka Bean has a pervasive scent.

The Food at Other Colonies

Each time one of the other Trinidad colonies was visited, a food sample was collected from below the nests, and sometimes from the nest themselves when they were accessible. On each occasion, hundreds of seeds were examined and an attempt was made to collect a sample showing the proportions in which the different kinds were present. Care was taken to collect only fresh seeds. Altogether, 18 samples were collected.

In general, the main kinds of fruit were the same as were being eaten by the birds at the Arima gorge colony in the same period, and they were in roughly the same proportions. Not a single seed was found at these other colonies that was not at some time found at the Arima gorge colony. Thus there is little doubt that the food of the Arima colony is typical of the Trinidad population as a whole. There were, however, some differences between the samples from these various colonies, which may be briefly summarized.

Oropouche Cave. — The most easterly cave, situated in an area of high rainfall, but at a low altitude. Eight samples were collected in seven different months. The composition was much the same as at the Arima colony, but *Beilschmiedia* was regular, sometimes in large numbers, and *Trattinickia* was never found. Two samples contained a smaller variety than was found at the Arima colony at the same time, the other six approximately the same variety.

Aripo Caves.—These are the highest caves, in montane forest. Six samples were collected in four different months. The composition was much the same as the Oropouche cave (again, *Trattinickia* was never found), but the variety was regularly less than at the Arima colony. For example in December, 1957, only *Jessenia* and *Beilschmiedia* could be found, although eight kinds of fruit were being taken at the Arima colony. The reason may lie partly in the poorer floristic composition of the montane forest (Beard, 1946).

La Vache Cave.—Two samples, both in August. The composition and variety was almost exactly the same as at the Arima colony at the same time.

Huevos Cave.— Two samples, in July and August. The composition was similar to that at the Arima colony, but *Ocotea caracasana* was abundant in the August sample (not present at the Arima colony; Table VIII), and *Livistona* was present in both samples. The latter was almost certainly obtained from Port-of-Spain gardens and parks.

It is noteworthy that *Trattinickia,* which was taken regularly by the Arima birds, was also present in three of the four La Vache and Huevos samples, but was never found in the samples from the Oropouche and Aripo caves. This strongly suggests that the tree is rare or absent east of the Arima Valley.

The Foraging Range

Extravagant claims have been made for the distances travelled by foraging Oilbirds in Venezuela (*e.g.,* 80 leagues—Funck, 1844), but without convincing evidence. For Trinidad the evidence, incomplete though it is, suggests that they can and do fly to places 15, or occasionally even 30 miles distant from the cave in search of food, but that foraging distances are usually much shorter.

Oilbirds have several times been seen feeding on the palm trees round the Queen's Park Savanna in Port-of-Spain, 14 miles from the Huevos cave and 8 miles from La Vache cave. The presence of numerous *Livistona* seeds in the Huevos samples, but not in the La Vache samples, suggests that the Huevos birds are involved. The La Vache birds would in any case have to cross hills of 1500 feet or more to reach Port-of-Spain, while the Huevos birds need not rise much above sea level. This is the longest foraging distance for which there is direct evidence, but almost certainly the Huevos birds at times fly farther afield. The forests within five miles of the Huevos cave are of dry monsoon type, far poorer than those to the east; so that the birds may often have to fly several miles to suitable feeding grounds. *Jessenia,* which was present in the Huevos samples, probably does not grow within 15 miles, and *Beilschmiedia,* of which one seed was found, has so far been found only on the Aripo massif, 30 miles to the east. Hence the Huevos birds must often fly considerable distances to feed, and they must be at an ecological disadvantage compared with the birds in the caves further east. It is not known whether they visit Venezuela, of which the nearest point is only nine miles away to the west.

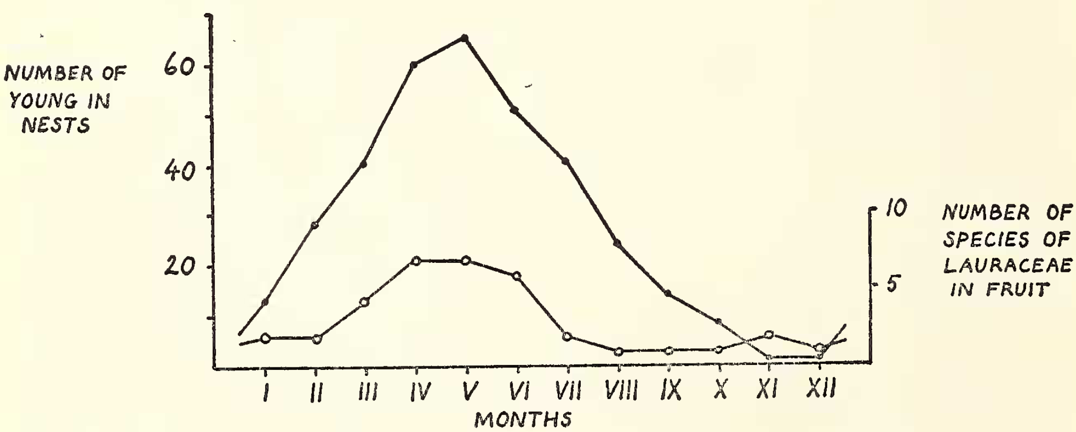
The Arima gorge birds visit Arima, five miles away, where they take *Livistona* fruits, and probably regularly visit the swampy forests between Arima and Valencia, eight or nine miles away, since *Jessenia* is not commonly found nearer than this. But they cannot regularly visit the montane forest of the Aripo massif, only five or six miles away to the east, since in over 112,000 seeds there were only three of *Beilschmiedia,* which forms an important part of the food of the birds of the Oropouche and Aripo caves. Conversely, *Trattinickia* was an important element in the food of the Arima gorge birds, but was never found in the samples from Oropouche and Aripo, showing that the birds from these caves do not normally visit the drier forests only a few miles to the west.

Availability of Food

If a fruit-eating bird is found to be taking a greater variety of fruits at some seasons than others, it could mean that highly acceptable food of several kinds is more abundant at that season than at others, or it could mean that its preferred food is scarce and it is having to seek other kinds. Conversely, few kinds of fruit in the diet might mean either that food is scarce, or that it is abundant and the bird is concentrating on the kinds that it most prefers. A bare analysis of food items in the diet may not enable one to decide between these two opposite possibilities. However, for the Oilbird we may safely conclude that when it is taking a large number of different kinds of fruit its food is especially abundant. The different fruits which they take and which make up the normal variety (the exceptional ones being left out of account) all recur regularly in their diet year after year, so cannot be regarded as foods to which they turn in times of shortage. Further, observations showed that they were taking the fruits as they became available in the forest, the periods when they were found in the food samples corresponding closely to the periods when the trees were observed to have ripe fruits. This again suggests a regular and normal exploitation of a seasonally varying food supply.

On this criterion of available variety, the Oilbird's food supply shows well-defined seasonal changes in abundance (Text-fig. 4). The greatest variety of food is available in the months April-June. It has already been shown that the breeding season is very long, and young birds may be in the nest in any month of the year. But there is a marked peak of laying in the months December-May, which results in more young birds being in the nests in the months March-June than at any other time (Text-fig. 4). This suggests that the breeding season is timed so that most young are in the nest when food is most abundant, though with such a long breeding season and extremely long nestling periods the adjustment cannot be very exact.

For the Venezuelan population, living in a more seasonal environment with a more marked dry season, the seasonal availability of food may show more marked fluctuations than in Trinidad, and the adaptation of breeding season to the fluctuating food supply may be more important. But precise data from Venezuela are



Text-fig. 4. Relationship between number of young in the nests in each year, all years combined (dots), and number of species of Lauraceae in fruit in each month (open circles).

lacking, both on the Oilbirds' breeding season and on the fruiting seasons of the food trees.

Regurgitation of Whole Fruits

As already mentioned in Part 1, the seed samples regularly contained a proportion of whole fruits which had been regurgitated intact, and others from which only part of the pericarp had been removed. A few of these were unripe fruits that had been picked by mistake, or in apparent anticipation of the time when they would be ripe (especially *Bactris cuesa* in March and April), but many were ripe and there was no obvious reason why they should not have been digested. In some months 10% or more of all fruits were intact but usually the proportion was between 1 and 5%. The percentage regurgitated whole showed no correlation with the availability of food, as measured by the number of food trees that had ripe fruit in that month, but was related to the state of breeding in the colony. In each year, the highest percentages of whole fruits were found towards the end of the main period when young were in the nests (July-September in 1958, April-May in 1960 and June-July in 1961). In 1959, when very few young were reared, the percentage of undigested fruits never rose above 3%.

The way in which the pericarps are digested and the seeds regurgitated is not properly understood. Young birds taken from the nest and kept under observation would regurgitate clean seeds and unaltered whole fruits in the same batch; no seeds were regurgitated with the pericarp in a half-digested or softened state, but some were regurgitated with it partially stripped off. The few stomach contents examined also showed a mixture of whole fruits and stripped seeds. Thus one must conclude that no digestion takes place in the stomach, but that the pericarps are gradually stripped off by the muscular action in the stomach and passed backward into the intestine, where digestion takes place. Once the pericarp has begun to come away from a seed, it will usually soon be stripped off, while another fruit eaten at the same time may still be intact.

Probably regurgitation begins to take place a certain length of time after the food has been eaten, and is largely under involuntary control except when an adult is feeding its young (Part 1, p. 42). By the time it begins to take place, most fruits will have been stripped of their pericarps, but a few may have remained intact; hence the regular occurrence of small numbers of whole fruits in the food samples at all seasons.

Nestlings taken out of the nest, and kept all day before being returned to the nest in the evening, regurgitated a high proportion of whole fruits: 118 (28%) of the total of 428. Regurgitation may perhaps have been abnormal, owing to the disturbance of being removed from the nest, but it seems likely that at any rate the larger nestlings, which receive very ample feeds, may normally regurgitate a rather high proportion of intact fruits. In addition the feeding process itself involves much strenuous activity by both adult and nestling (Part 1, p. 41), and some fruits may be dropped as the food is passed from adult to young. It is thus not surprising that late in the nestling period a rather large number of whole fruits are found on the nests and the slopes below the nests. From the ecological viewpoint, it suggests an ample food supply, since if the supply of food were often critical it is unlikely that such wasteful behavior could persist.

Food Value of the Fruits Eaten, and Its Ecological Implications

Oilbirds range widely over the forest at night, and of the many fruits that are available they take only a few kinds, avoiding many others that are eaten by diurnal fruit-eating birds. Almost without exception, as already mentioned, the fruits which they regularly take are kinds that have a firm, in some cases hard, non-succulent pericarp, enclosing a single seed. From this it seems probable that succulent fruits have insufficient food value for their weight to be an economical food for Oilbirds, which not only feed on the wing but must fly considerable distances to their food trees.

To test the point further, the food values of some of the more important kinds of fruit eaten by Oilbirds were determined, through the courtesy of Professor J. K. Loosli of the New York State College of Agriculture. They are given in Table XI, which also lists for comparison the equivalent values for some common succulent fruits eaten by birds and men. It will be seen that the fruits taken by Oilbirds have an extremely high fat content and on average a markedly higher protein content than the succulent fruits; the fat:protein ratio is in fact much like that of a nut kernel. (In fat content they are exceeded by two well-known fruits, the avocado pear (59%) and the olive (68%), but the fat content of these may well have been increased by artificial selection. They belong to families which are represented in the Oilbird's diet, the Lauraceae and Oleaceae).

The food value of the fruits taken by Oilbirds in comparison with succulent fruits is even

TABLE XI. ANALYSIS OF DRIED PERICARPS OF FRUITS EATEN BY OILBIRDS, AND SOME OTHER FRUITS

		Percentage composition		
		Protein	Fat	Carbohydrates, ash and crude fiber
Fruits regular in Oilbird's diet	LAURACEAE			
	Cinnamomum elongatum	9	44	47
	Ocotea oblonga	11	19	70
	Ocotea wachenheimii	14	34	52
	BURSERACEAE			
	Dacryodes sp.	11	24	65
	PALMAE			
	Bactris cuesa	13	39	48
	Jessenia oligocarpa	5	26	69
Fruits occasionally taken but generally avoided	LAURACEAE			
	Ocotea canaliculata	8	34	58
	ANACARDIACEAE			
	Tapirira guianensis	5	7	88
Some succulent fruits	Apple	2	Tr.	98
	Fig	5	Tr.	95
	Gooseberry	4	Tr.	96
	Grape	4	Tr.	96
	Red currant	6	Tr.	94

NOTE: Data for the first seven supplied by Professor J. K. Loosli, Cornell University, *in litt.;* percentages for *Tapirira* by Mr. J. S. Leahy, Huntingdon Research Centre, England (*in litt.*); percentages for last five reworked from data given in McCance & Widdowson (1946).

greater than is suggested by this table, as their water content is lower. In most succulent fruits the water content of the pericarp is between 75 and 85%, while that of the palms eaten by Oilbirds is probably less than 50% (exact figures not available), that of *Dacryodes* 60%, and that of *Ocotea wachenheimii* about 75%. Thus there seems little doubt that Oilbirds select the kinds of fruit that they do primarily because their food value is, for fruits, unusually high.

It may be noted that, although the palm fruits have drier pericarps than the Lauraceae, their seeds are relatively larger, weighing 54-69% of the total weight of the fruit in the three most important species, as against 33-42% in the three species of Lauraceae for which there are data (Table XII). Thus weight for weight they yield approximately the same amount of nutritive matter.

It was mentioned in Part 1 that many of the trees on which Oilbirds feed are spicy or aromatic, and it was suggested that the olfactory sense may be important in enabling them to locate the food trees (see also Bang, 1960, for anatomical evidence supporting this suggestion). The situation in the Arima Valley in March-May, 1961, was particularly illuminating in this respect. Three common species of Lauraceae were in fruit at the same time, *Cinnamomum elongatum, Ocotea oblonga* and *O. canaliculata*. The first two had fruited regularly in previous years (Table VIII), but *O. canaliculata* had not been observed in fruit in the lower part of the Arima Valley, and certainly cannot have fruited prolifically. (Higher in the valley, one tree under observation had produced a little fruit in 1958 and 1959). The Oilbirds, as usual, took large quantities of *Cinnamomum* and *O. oblonga* fruit, but only one seed of *O. canaliculata* was found among the thousands examined. Samples of dried pericarp of all three were analyzed (Table XI). In fat content *O. canaliculata* was intermediate between the other two, being exactly the same as *O. wachenheimii,*

TABLE XII. WEIGHTS OF FRUITS EATEN BY OILBIRDS

	Number weighed	Mean weight (gm.)	Mean weight of pericarp (gm.)
LAURACEAE			
Cinnamomum elongatum	5	0.6	0.4
Ocotea caracasana	2	9.5	5.0
Ocotea wachenheimii	16	3.3	1.9
BURSERACEAE			
Dacryodes sp.	10	2.8	1.3
Trattinickia rhoifolia	2	1.5	1.0
PALMAE			
Bactris cuesa	10	4.1	1.9
Euterpe langloisii	20	1.3	0.4
Geonoma vaga	15	0.17	0.10
Jessenia oligocarpa	6	16.8	6.2
Livistona chinensis	8	2.0	0.9

which is much eaten. In protein content it was only 1% lower than *Cinnamomum. O. canaliculata* would thus seem from its nutritional value to be a perfectly suitable food for Oilbirds. There was, however, a striking difference between the three samples: the pericarp of *Cinnamomum* was highly aromatic, that of *O. oblonga* noticeably so, but that of *O. canaliculata* absolutely non-aromatic. These differences were noted without exception by several persons who where presented with the samples in random order and asked to comment on them.

A further comparison was made between the three "gommiers," *Dacryodes* and *Trattinickia* which are much eaten, and *Tapirira guianensis* which is avoided, though locally it is the commonest of the three. The local name reflects a general similarity between these trees, all of which produce gum from the bark, have rather similar compound leaves and bear bunches of fruit of much the same size and type. The Oilbirds' selection of the first two species and avoidance of the third may have the same cause as in the three Lauraceae: *Dacryodes* and *Trattinickia* are aromatic, but *Tapirira* is not. However, analysis of *Tapirira* fruits (Table XI) showed that their fat and protein content is markedly low compared with the fruits that are regularly eaten, so that it is probably not an economical fruit for Oilbirds to take.

The palms on which Oilbirds feed are not aromatic. It seems likely that they are located visually, a method which would be easier for palms, with their characteristic shape, than for dicotyledonous trees.

These facts strongly suggest that, while the food value of the fruit is of primary importance, in searching for suitable food trees other than palms Oilbirds are guided to an important degree by the olfactory sense. This is in the main an efficient method, since most of the trees on which they feed, in the families Lauraceae and Burseraceae, are aromatic; but it results in their missing some species which from the nutritional standpoint are suitable.

In Part 1, p. 42, it was shown that the three young Oilbirds which were investigated ate about one-quarter to one-third of their bodyweight in the course of a night. Using these figures, and the known food values of the fruits eaten, we can make a rough assessment of the total amount of protein, fat and carbohydrate eaten by a nestling Oilbird in the course of its growth. We may consider only the first 70 days of its nestling period, when it is increasing in weight.

If we assume that it eats one-third of its weight every night (though this figure may well be a little too high for the last 20 days), and take an average growth-curve from 14 gm. at hatching to 600 gm. at 70 days (Part 1, Table III), we find that in the course of its first 70 days a nestling Oilbird will eat about 7,600 gm. of fruit. Using the mean figure for the Lauraceae (Table XII), this corresponds to 4,560 gm. of pericarp, and to 1,370 gm. of dried pericarp (using figures for *Ocotea wachenheimii*). Analysis of the percentage composition of dried pericarp showed that protein content was around 10% for most species, fat content about 30%, and carbohydrate content about 35%. Thus 1,370 gm. of dried pericarp will give about 137 gm. of protein, 410 gm. of fat, and 480 gm. of carbohydrate.

The total nitrogen in proteins is about 16% by weight. Thus 137 gm. will contain about 22 gm. of nitrogen. It is not possible to make more than a rough assessment of the total nitrogen in a 70-day nestling Oilbird, but the following figures may be used provisionally. Probably some 250 gm. of the total weight consists of fat, and the remaining 350 gm. represents the nitrogen-containing fraction, as the weight of the adult, which has little fat, is on average 415 gm. and the body dimensions, muscular development and feathering of the 70-day nestling are somewhat less than in the adult. No figures have been found for the total protein content of a bird, but using the figures for fresh meat (around 20%) and allowing a reduction for blood and bone, we may take 15% as a reasonable figure. Thus we may estimate that a 600 gm. nestling Oilbird will contain roughly 8.5 gm. of nitrogen (350 gm. × 15% × 16%). This figure agrees well with an independent estimate from data given by Rubner (quoted in Brody, 1945). According to Rubner, one kg. of normal body substance (*i.e.*, including all organs in due proportion) contains about 30 gm. of nitrogen. Consequently 350 gm. will contain about 10.5 gm.

In the absence of data on the nutritional value and amino-acid composition of the proteins in the nestling Oilbird's diet, we can do no more than guess whether an intake of 22 gm. of nitrogen would be adequate to produce 9 or 10 gm. of nitrogen in the body. But the efficiency of utilization of dietary nitrogen derived wholly from fruit pericarps, over a period of 70 days, could hardly be expected to exceed 50%, which suggests that the young Oilbird is growing as fast as is possible on such a diet.

Turning to the energy requirements of the growing Oilbird, we may make another rough calculation. The total intake of food, as estimated above, yields 6,343 calories (on the basis of 4.1 cal. per gm. of carbohydrate, 9.3 cal. per gm. of fat, 4.1 cal. per gm. of protein; Best & Taylor, 1949). The calorific value of a 70-day Oilbird weighing 600 gm. is not exactly known, but it may be estimated at 3,025 cal., on the basis of 9.3 cal. per gm. of fat and 2 cal. per gm. of the rest of body-substance. This gives a gross efficiency of growth, in respect of consumed metabolic energy, of about 48%. Brody (1945) quotes equivalent figures for rats and chickens: for rats, gross efficiencies up to 13.6%; for slow-growing chickens, gross efficiencies up to about 20%. The apparently very high gross efficiency of the nestling Oilbird is probably made possible by the development of the thick insulating layer of fat, the growth of a thick covering of down and relative inactivity.

These calculations, rough though they are, probably have enough validity to justify the conclusion that on a diet of pericarps of palm and lauraceous fruits young Oilbirds could not obtain enough nourishment to develop any faster than they do. Thus the very long nestling period may be regarded primarily as an adaptation to the very specialized diet, as provisionally suggested in Part 1, p. 44. This adaptation could not have been acquired unless the birds had available to them nest-sites safe from most natural predators.

This conclusion rests on the assumptions that the parents could not provide more food for the nestlings, or that if they could, the nestlings would not be able to deal with a greater quantity of bulky food per day. Neither of these assumptions can be tested on present evidence, but the facts that Oilbirds have often to fly several miles for food, that their flight-speed in level flight is not high, and that they spend up to four hours apparently feeding themselves before they return with food for the young (Part 1, p. 41), all suggest that the three or four feeds in the night that were recorded are as many as are normally possible under the circumstances.

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Summary

The present adult population of Oilbirds in Trinidad, in the eight known colonies, is estimated to be 1,460. Five small colonies have been exterminated in recent years. The population is considered to be in no immediate danger, but is potentially vulnerable.

The breeding season is very long, extending from December to September, but nearly all clutches are laid before June. The moult takes place mainly in June-November, but it lasts so long that in some individuals it almost certainly overlaps the beginning and/or end of the breeding cycle. There is evidence that birds may begin a second wing-moult before the first is complete.

Clutch-size varies from 1 to 4 eggs, the mean being 2.7. It was found to decrease in the course of the breeding season, probably in correlation with decreasing abundance of food.

Nearly 50% of observed nestings were successful, earlier nestings being more successful than later ones. The causes of failure were various; there was no evidence of starvation of nestlings except perhaps occasionally in the first few days.

An analysis is given of 112,000 seeds collected from the Arima gorge colony. The important fruits comprised 7 species of palms, 8 of Lauraceae, 2 of Burseraceae, and 1 of Araliaceae. Two important palms provided a more or less steady supply of food throughout the year: the Lauraceae were nearly all regularly seasonal. Evidence is given that Oilbirds may fly up to 30 miles for their food, but foraging distances are usually much shorter.

The greatest variety of food is available in the months April-June, corresponding to the period when most young are in the nest. In all months of the year, a proportion of the fruits are regurgitated whole, rising to 10% or more in the latter part of the breeding season.

The food values of some of the chief foods are analyzed, and it is concluded that on a diet of fruit pericarps young Oilbirds could not develop much faster than they do. The extremely long fledgling period is thus primarily an adaptation to the specialized diet.

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APPENDIX

SYSTEMATIC LIST OF THE OILBIRD'S FOOD TREES

The order and nomenclature follow Beard (1946), with alterations and additions as noted.

LAURACEAE

Aiouea schomburgkii Meissn.
Aniba firmula (Nees) Mez
Aniba panurensis Mez, listed in Beard, is a synonym.
Aniba trinitatis (Meissn.) Mez
Beilschmiedia sulcata (R. & P.) Mez
Genus and species new to Trinidad.
Licaria guianensis Aubl.
New to Trinidad.
Nectandra martinicensis (Jacq.) Mez
Nectandra membranacea (Sw.) Griseb.
Nectandra kaburiensis Kosterm.
Listed in Beard as *N. surinamensis* Mez.
Ocotea canaliculata (Rich.) Mez
Ocotea caracasana (Nees) Mez
New to Trinidad.
Ocotea oblonga (Meissn.) Mez
Ocotea wachenheimii R. Benoist
Ocotea arenaensis R. L. Brooks, listed in Beard, is a synonym.
Cinnamomum elongatum (Vahl) Kosterm.
Listed as *Phoebe elongata* (Vahl) Nees in Beard. *Phoebe* is synonymous with *Cinnamomum*, fide Kostermans.

MYRISTICACEAE

Virola surinamensis (Rol.) Warb.

BURSERACEAE

Dacryodes sp.

Specific determination depends on specimens with flowers, which have not yet been obtained. Previously known from Trinidad on the basis of one old specimen, but locally well-known as "mountain incense" or "gommier montagne," and referred to under the latter name by Beard.

Trattinickia rhoifolia Willd.

MALPIGHIACEAE

Byrsonima spicata (Cav.) Rich.

ANACARDIACEAE

Tapirira guianensis Aubl.

ARALIACEAE

The atypical fruit which remained unidentified (p. 212) is referred to this family with reasonable certainty by Mr. N. Y. Sandwith (Kew) and Dr. A. C. Smith (U.S. National Museum), who were sent detailed drawings of the mature fruit. The latter suggests the genera *Dendropanax* or *Schefflera* as being the most likely.

SAPOTACEAE

Pouteria minutiflora (Britt.) Sandwith

OLEACEAE

Linociera caribaea (Jacq.) Knobl.

BORAGINACEAE

Cordia bicolor DC.
Cordia lockhartii Kuntze, listed in Beard, is a synonym.

PALMAE

Bactris cuesa Crueg.
Euterpe langloisii Mart.

No consistent differences could be found between the many *Euterpe* seeds and fruits in the food samples. All appeared to come from the common *Euterpe* of the forests of the Northern Range, for which the name *langloisii* may provisionally be used. The species have been very finely split (Bailey, 1947).

Geonoma vaga Griseb. & Wendl.
Jessenia oligoarpa Griseb. & Wendl.
Livistona chinensis R. Br.
Roystonea oleracea (Jacq.) Cook

EXPLANATION OF THE PLATES

PLATE I

FIG. 1. Seeds and whole fruit (upper right) of *Jessenia oligocarpa*. (Millimeter scale is shown in this and the next five figures.)

FIG. 2. Seeds of *Euterpe langloisii*.

PLATE II

FIG. 3. Seeds of *Livistona chinensis*.

FIG. 4. Seeds of *Trattinickia rhoifolia*.

PLATE III

FIG. 5. Seeds of *Ocotea wachenheimii*.

FIG. 6. Seeds of *Aniba firmula*.

PLATE IV

FIG. 7. Oilbird nests in the Arima gorge, showing eggs and small young, and seeds of *Ocotea caracasana* (smooth, shiny and spindle-shaped) and *Jessenia oligocarpa* (larger, streaked) round the edges of the nests.